Management and Conservation Article

Factors Affecting Songbird Nest Survival in Northern Mixed-Grass Prairie

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ABSTRACT Factors associated with the nest survival of mixed-grass prairie passerines are not well known, especially in the context of contemporary grassland management. We documented the nest survival of clay-colored sparrows (*Spizella pallida*), savannah sparrows (*Passerculus sandwichensis*), and bobolinks (*Dolichonyx oryzivorus*) in managed prairie in northwestern North Dakota, USA. We used logistic exposure models and an information-theoretic framework to estimate nest survival and evaluate support for mechanisms (grazing, temporal factors, nest parasitism, nest-site vegetation, and nest-patch factors) relevant to nest survival. Survival for the entire nesting interval (23–28 days) was low for clay-colored sparrow (18.2%), savannah sparrow (15.5%), and bobolink (3.5%). We found support for a cubic effect of nest age; survival of savannah and clay-colored sparrow nests was greatest during mid-incubation and least during the mid-nestling period. Parasitized clay-colored sparrow and bobolink nests had greater survival rates than nonparasitized nests. Nest survival of clay-colored sparrows increased with increasing vegetation height and density. For savannah sparrows, nest survival was lower when cattle were present than when cattle were absent. Characteristics of the nest patch did not have strong effects based on model coefficients and confidence intervals, though they appeared in many of the most supported models. Positive effects of vegetation height and density on nest survival of clay-colored sparrows and negative effects of cattle presence on nest survival of savannah sparrows suggest some detrimental effects of grazing. However, the need to restore and maintain intact prairies likely warrants the continuation of cattle grazing on conservation lands.

KEY WORDS *Dolichonyx oryzivorus*, livestock grazing, mixed-grass prairie, nest survival, *Passerculus sandwichensis*, passerines, prairie restoration, *Spizella pallida*.

The ecological integrity of North American prairies has been substantially degraded. Native grasslands have been eliminated, primarily by cultivation, and anthropogenic alterations of natural disturbance regimes (e.g., fire and grazing) have created significant departures from presettlement ecological conditions on many remaining grasslands (Samson et al. 2004, Grant and Murphy 2005). The spread of nonnative vegetation has further transformed large portions of these ecosystems (Grilz and Romo 1995, Christian and Wilson 1999).

Grassland breeding bird populations have been adversely affected by these changes, with several species exhibiting declines in recent years (Houston and Schmutz 1999, Peterjohn and Sauer 1999). Although it is more intact than the tall-grass prairie ecosystem, the northern mixed-grass prairie is at risk from exotic invasions, interruptions of natural disturbance mechanisms, and habitat loss and fragmentation (Bragg and Steuter 1995, Samson and Knopf 1996). On northern mixed-grass prairies protected for conservation, active management such as grazing and burning is necessary to restore and maintain their ecological integrity. At Lostwood National Wildlife Refuge (NWR) in northwestern North Dakota, USA, a prescribed burn

program was implemented in the late 1970s to reduce exotic and woody vegetation (United States Fish and Wildlife Service 1998). Because fire was not adequately promoting native grasses or reducing exotic smooth brome (*Bromus inermis*), rotational grazing was added in the 1990s. Grazing may be controversial on conservation lands (e.g., Kirby et al. 1992, Fleischner 1994) but in systems that evolved with significant grazing, the prolonged absence of grazing can be detrimental (Hobbs and Huenneke 1992, Fuhlendorf and Engle 2001) and long-term benefits of restoration may offset short-term negative impacts (Kirby et al. 1992).

To help clarify how grazing affects passerines breeding in the northern mixed-grass prairie, we investigated the influence of rotational grazing, as used for grassland restoration in the northern mixed-grass prairie, on nest survival of 3 passerine species: clay-colored sparrows (*Spizella pallida*), savannah sparrows (*Passerculus sandwichensis*), and bobolinks (*Dolichonyx oryzivorus*). We used an information-theoretic approach to evaluate 5 hypotheses concerning nest survival. We hypothesized a negative effect of grazing on nest survival via trampling of nests (Temple et al. 1999, Renfrew and Ribic 2003) or altering the suitability of nest sites (Kruse and Bowen 1996, Temple et al. 1999). Because predation has been identified as the leading cause of nest failure in the northern mixed-grass prairie (Pietz and Granfors 2000, Davis 2003), we also considered other factors that might affect nest vulnerability to predation: nest-patch characteristics, nest-site vegetation, temporal

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factors, and parasitism. Certain landscape features near the nest site (i.e., nest-patch characteristics) may affect the probability a nest is depredated by attracting or discouraging predators (Budnik et al. 2002). Linear edges such as roads can increase the probability of a traveling predator's presence (Dijak and Thompson 2000), whereas features such as trees and shrubs can provide cover for certain predators (Winter et al. 2000, Renfrew and Ribic 2003, but see Grant et al. 2006). We hypothesized that increasing amounts of edge and predator-increasing cover would negatively affect nest survival. Vegetation at nest sites has been shown to influence the probability of predation (Martin 1992, Burhans and Thompson 1998); we hypothesized an increase in nest-site vegetation height and density, concealment, and litter depth would positively impact survival by concealing nests from predators. Also, temporal factors, such as date and age or stage of the nest, have been associated with differing nest survival in other studies (Pietz and Granfors 2000, Burhans et al. 2002, Davis 2005, Grant et al. 2005). Because recent evidence indicates survival varies nonlinearly with nest age (Davis 2005, Grant et al. 2005), we hypothesized nest survival would be curvilinear. Because nests initiated early in the season can be more successful (Grant et al. 2005), we hypothesized increasing day of year would be negatively associated with nest survival. Brown-headed cowbirds (*Molothrus ater*) are known to impact the survival of songbird hosts by egg removal (Arcese et al. 1996, Granfors et al. 2001), inducing abandonment (Smith et al. 2003), and via cowbird chicks out-competing host chicks (Dearborn et al. 1998, Davis and Sealy 2000) or attracting predators with louder, more frequent begging (Robinson et al. 1995, Dearborn 1999). Therefore, we expected cowbird parasitism to have a strong negative effect on the survival of these species.

STUDY AREAS

We searched for nests on Des Lacs NWR, Lostwood NWR, and Coteau Prairie Waterfowl Production Area (WPA) in northwestern North Dakota. Des Lacs NWR (7,900 ha), in Burke and Ward counties, consisted of connected management units (HB units) on both sides of the Des Lacs River. Native mixed-grass prairie vegetation was drastically reduced after invasion by smooth brome and Kentucky bluegrass (*Poa pratensis*), and proliferation of native woody vegetation, particularly western snowberry (*Symphoricarpos occidentalis*) and silverberry (*Elaeagnus commutata*) in the uplands, and quaking aspen (*Populus tremuloides*) around wetlands. We used 4 HB units (HB2, 145 ha; HB3, 85 ha; HB4, 97 ha; and HB5, 97 ha) as study sites in 2002 and 2003. We added a fifth unit (HB35, 470 ha) in 2003.

Lostwood NWR (11,000 ha) in Burke and Mountrail counties was characterized by rolling topography and numerous wetland basins. Possibly due to diverse microsites, longer prescribed burn history, and lower edge–interior ratio, Lostwood had fewer patches of smooth brome, Kentucky bluegrass, and woody cover than Des Lacs. Uplands at Lostwood were dominated by native warm- and cool-season grasses, and prairie forbs. We used the eastern 157 ha of the Green Needle management unit in the central portion of the refuge as our study site. Coteau Prairie WPA (1,100 ha), 6 km southeast of Lostwood NWR in Mountrail County, had similar biotic and abiotic characteristics as this refuge. We used 166 ha in the south-central portion of this WPA.

METHODS

Data Collection

We searched for nests from mid-May through early July 2002 and 2003. We located nests by dragging (on foot) weighted, 10-m to 15-m nylon ropes with steel cans attached at 1-m intervals and searching near flushed birds (Labisky 1957). We also located nests via incidental discovery. Upon discovery, we recorded age and number of host and brown-headed cowbird eggs or young in each nest. We aged eggs with candling tubes (Lokemoen and Koford 1996) and used a Global Positioning System (GPS) to obtain geographic coordinates of nests. We marked nests with 2 1-cm-diameter fiber rods placed 2 rod-lengths north and south of nests. We measured nest concealment by placing an 8-sectioned, laminated paper disk on the nest, and counting the number of sections $\geq 50\%$ visible at 1.5 m above ground level directly above the nest (Davis and Sealy 1998). We visited nests every 4–5 days until 2–4 days prior to fledging, when we visited daily. We assigned final fates based on adult behavior, projected age and evidence (e.g., droppings, call notes, sightings) of nestlings, or any egg or chick remains. At nest termination, we recorded litter depth by inserting a marked probe to ground level and recording the depth in centimeters of dead, horizontal vegetation that formed a continuous layer to ground level. We also recorded a visual obstruction reading (VOR) in decimeters by placing a marked pole (Robel et al. 1970) at the north edge of the nest and averaging observed obstruction from the 4 sides when observed from 1 m high at a distance of 4 m.

We randomly assigned portions of 5 study areas (4 at Des Lacs, 1 at Coteau Prairie) as grazed with an adjacent ungrazed area. We paired 2 land units on Des Lacs, with HB3 being a nongrazed area and adjacent HB4 grazed. We did not randomly assign grazing treatment on Lostwood because adequate water for livestock was only present on the western side. We divided each grazed area into 3 equal-sized paddocks (cells). Stocking rates followed guidelines recommended by the United States Soil Conservation Service (1984): 0.20–0.28 animal unit months/ha. With slight variation, cattle grazed all cells following a 2-week rotational schedule with grazing schedules offset by 2 weeks between years. This grazing scheme was consistent with grassland restoration practices at other northern Great Plains national wildlife refuges.

We used a GPS to map tall (>1.5-m) woody cover, rock piles, and surface water. We digitized roads, row-crop edges, and edges of draws in a Geographic Information System from aerial photos and topographic maps. We merged these features with relevant, preexisting data layers to make 2 data layers: cover and edge. The cover layer consisted of the sum of the areal extent (m^2) of water sources, woody cover, and

rock piles. The edge layer consisted of roads, grassland or crop edges, and edges of draws. We calculated cover and edge density (m edge length/ha) within 100 m (3.14 ha) of each nest.

Data Analysis

We used an information-theoretic approach (Burnham and Anderson 2002) to evaluate hypotheses affecting nest survival. We assessed 5 a priori hypotheses regarding temporal, parasitism, grazing, nest-site vegetation, and nest-patch effects using 4 models that evaluated variables potentially affecting nest survival.

The temporal-parasitism model included day of year and age of nest (no. of days since the first egg was laid). We modeled a squared and cubic effect of age, because recent evidence indicates survival varies nonlinearly with nest age (Grant et al. 2005). We classified parasitism as binary (0, 1), where 1 indicated a nest with ≥ 1 viable brown-headed cowbird egg or young at that nest visit.

The grazing model contained variables quantifying instantaneous, cumulative, and total system impacts on nest survival. Interval grazing was binary: zero indicated no grazing, whereas one indicated cattle grazing in the cell during the nest-check interval. Days grazed was the number of days cattle had grazed the cell that year prior to that nest check; we coded nests in ungrazed cells zero. We did not include days grazed in the grazing model for bobolinks because the smaller sample size could not support as complex a model as the other 2 species. Finally, we evaluated an overall impact of rotational grazing by assigning a grazing treatment effect (one for grazed, zero for ungrazed) to indicate whether a nest was located on a grazed or ungrazed site.

The nest-site vegetation model contained the measurements that described nest concealment, VOR, and litter depth. Lastly, the nest-patch model included variables for cover and edge. We evaluated support for each of these models, all 2- and 3-way combinations of these models, a global model that included all variables, and a null model with no variables, for a total of 16 models/species. Each variable appeared in 8 of these models.

We used the logistic exposure method (Shaffer 2004) implemented using PROC NLMIXED (SAS Version 8.0; SAS Institute, Cary, NC) to model the effects of the previously described factors on nest survival. We considered a nest successful during an observation interval if it contained viable host eggs or young. We excluded from analysis nests that contained only brown-headed cowbird eggs or young when found, or were abandoned in the laying stage (i.e., possibly due to investigator disturbance). To account for potentially correlated fates of nests within the same site in the same year, we included a single random effect that combined site and year. Only year was used as a random effect for bobolinks because their nests were located primarily (73%) on Des Lacs. We used a likelihood-ratio test to compare the global model to the null model and proceeded with model selection because for all species the global model had a significantly greater likelihood than the

null model (clay-colored sparrow: $\chi^2 = 217.69$, df = 13, $P < 0.005$; savannah sparrow: $\chi^2 = 91.29$, df = 13, $P < 0.005$; bobolink: $\chi^2 = 54.96$, df = 13, $P < 0.005$). We ranked models from most to least supported based on Akaike's Information Criterion (AIC) scores. When no single model was clearly most supported (i.e., model selection uncertainty occurred), we employed model-averaging (Burnham and Anderson 2002), using models with $\Delta AIC \leq 2$. We deemed explanatory variables to be those with interpretable effects whose with-odds-ratio confidence intervals did not overlap one (i.e., equal odds; Hosmer and Lemeshow 2000). We report model-averaged parameter estimates with their standard errors, odds ratios, and associated confidence intervals.

We plotted species-specific daily survival rates (DSRs) as a function of variables with strong effects to demonstrate effects on nest survival. We generated model-averaged DSRs for selected variables following the approach of Shaffer and Thompson (2007). To predict DSRs, we set the variable of interest at incremental levels within the range of our data for continuous variables, and 0 and 1 for binary variables. To control for the effects of other variables in the model, we set the variables at their sample means. When model-averaging was warranted, we model-averaged predicted DSRs from models with $\Delta AIC \leq 2$. We predicted an overall DSR and nesting-interval survival rate for each species based on nest intervals of 23 (clay-colored sparrows), 25 (savannah sparrows), or 28 (bobolinks) days. Because of the nonlinear effect of nest age (see results), we estimated DSRs and confidence limits for each day of the nest cycle, while holding all other variables at their sample means, and took the product of the daily estimates and confidence limits for an interval rate, and present these as both a daily rate and interval rate.

RESULTS

We monitored 496 clay-colored sparrow nests in 2002 and 2003. Predation was the leading cause of nest failure, accounting for 272 of 316 (86.1%) failures. Cattle trampling accounted for 10 of 316 (3.2%) nest failures. Of 496 nests, 84 (16.9%) were parasitized. The most supported models all included temporal effects; however, no single model had overwhelming support. Two models were well-supported with $\Delta AIC \leq 2$ (Table 1). Nest survival was highest during middle incubation (day 9) and lowest midway through the nestling stage (day 20; Fig. 1). Of 13 parameters, 4 had model-averaged estimates with odds-ratio confidence intervals that did not overlap one (Table 2). Increasing vegetation height and density (Fig. 2) and parasitism (Fig. 3) were associated with increased survival. The parameter estimate for grazing during the nest interval was negative, but the odds-ratio confidence interval overlapped one (Table 2). The interval nest-survival rate was 18.2% (95% CI = 8.6–37.3%).

We monitored 236 savannah sparrow nests in 2002 and 2003. Predation was the leading cause of nest failure, accounting for 148 of 167 (88.6%) failures. Cattle trampling was responsible for 2 of 167 (1.2%) failures. Of 236 nests, 46

Table 1. Model-selection results for 16 logistic exposure models of nest survival of bobolinks, clay-colored sparrows, and savannah sparrows in northwestern North Dakota, USA, during 2002–2003 based on 302, 1,652, and 784 nest-observation intervals of 108, 496, and 236 nests of bobolink, clay-colored sparrow, and savannah sparrow, respectively. Models are ranked based on Akaike's Information Criterion (AIC), based on $-2 \times$ log likelihood (L) and the number of parameters (K) in the model, and Akaike weights (w_i). Only models with ΔAIC ≤ 2 are presented.

Species	Model	$-2(L)$	K	AIC	ΔAIC	w_i
Bobolink	Temporal[a]	307.66	7	321.66	0.00	0.53
Clay-colored sparrow	Temporal + vegetation[b]	1,508.48	10	1,528.48	0.00	0.41
	Temporal + vegetation + grazing[c]	1,503.21	13	1,529.21	0.76	0.28
Savannah sparrow	Temporal + vegetation + grazing	742.76	13	768.76	0.00	0.36
	Temporal + grazing	749.76	10	769.76	0.93	0.23
	Global[d]	740.31	15	770.31	1.61	0.16

[a] Temporal includes age + age^2 + age^3 + date + parasitized.
[b] Vegetation includes visual obstruction + litter depth + initial overhead concealment.
[c] Grazing includes treatment + days grazed + interval grazing.
[d] Global includes all variables.

(19.5%) were parasitized. No single model had overwhelming support; 3 models were well-supported with ΔAIC ≤ 2 (Table 1). Three parameters had model-averaged estimates with odds-ratio confidence intervals that did not overlap one (Table 2). Nest survival again was curvilinear over time, being lowest in the early to mid-nestling stage (i.e., nest age 20–22; Fig. 1). The odds ratio for interval grazing indicated a negative effect of the presence of cattle (Table 2) and predicted DSR was substantially less during intervals with grazing than those without (Fig. 4). The interval nest-survival rate was 15.5% (95% CI = 5.6–40.5%).

We monitored 108 bobolink nests in 2002 and 2003. Predation was the leading cause of nest failure, accounting for 73 of 91 (80.2%) failures. Cattle trampling accounted for 1 of 91 (1.1%) nest failures. Of 108 nests, 43 (39.8%) were parasitized. Only the temporal model had ΔAIC ≤ 2 (Table 1). One parameter, parasitism, had a model-averaged estimate with an odds-ratio confidence interval that did not overlap one (Table 2). Parasitism was associated with increased probability of surviving an interval (Fig. 3). The interval nest-survival rate was 3.5% (95% CI = 0–11.6%).

DISCUSSION

For clay-colored sparrows and savannah sparrows, nest survival was curvilinear. Although Davis (2005) found support for a linear, negative effect of nest age for savannah sparrows, Grant et al. (2005) reported a similar curvilinear relationship between nest survival and nest age for clay-colored and vesper sparrows (*Pooecetes gramineus*). Decreasing survival later in incubation and early in brood rearing could be related to increased parental activity near the nest (e.g., Martin et al. 2000) or simply increased risk associated with longer exposure (Grant et al. 2005). Early nestling stage was more hazardous than late nestling in our study, whereas predation risk for clay-colored sparrows and other northern mixed-grass prairie passerines increased with nestling age in southeastern North Dakota (Pietz and Granfors 2000). These patterns may reflect differences in predator dynamics among sites.

Greater survival for parasitized clay-colored sparrow and bobolink nests, although contrary to our expectation, is not unheard of (Arcese et al. 1996, Eckerle and Breitwisch 1997). Because brown-headed cowbirds and other northern mixed-grass prairie passerines co-evolved (unlike many hosts in the cowbird's recently expanded range), cowbirds could be adept at choosing nests they perceive as likely to be successful, thus maximizing their chances of producing offspring. Also, some (Arcese et al. 1996, Hoover and Robinson 2007) have posited that cowbirds are not likely to depredate nests they have parasitized; although cowbirds are not the dominant predator of mixed-grass prairie songbirds, they do comprise a significant percentage of recorded
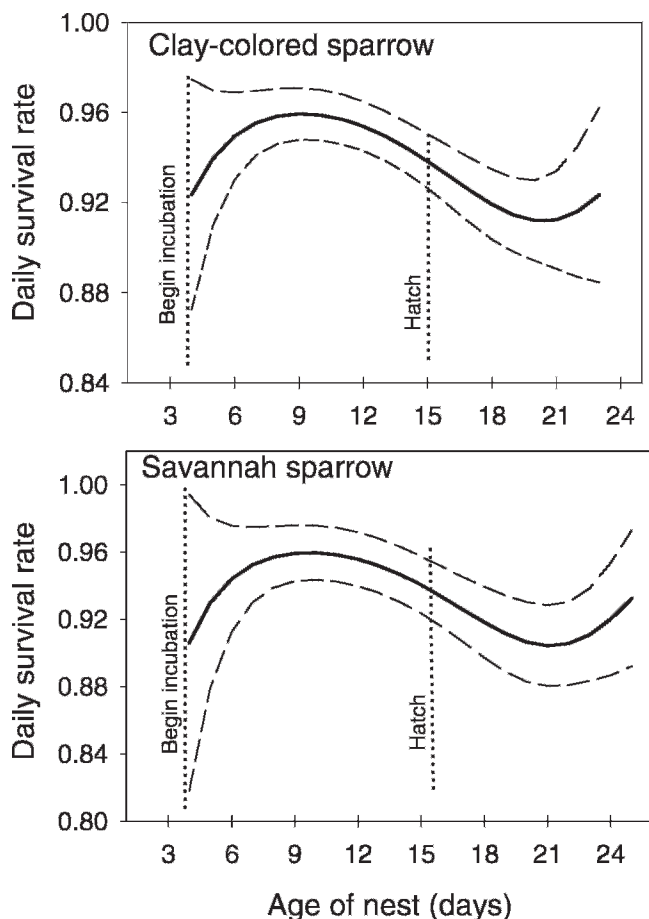

Figure 1. Effect of nest age on daily survival, with 95% confidence intervals, for clay-colored sparrow (upper) and savannah sparrow (lower) nests in northwestern North Dakota, USA, 2002–2003.

Table 2. Model-averaged parameter estimates, unconditional standard errors, and odds ratios with 95% confidence intervals for well-supported (Akaike's Information Criterion within 2 of most supported model; ΔAIC ≤2) logistic-exposure models of nest survival of bobolink, clay-colored sparrow, and savannah sparrow nest survival in North Dakota, USA, during 2002–2003. The number of nest-observation intervals for bobolink, clay-colored sparrow, and savannah sparrow were 302, 1,652, and 784, respectively.

Species	Parameter	Estimate	SE	Odds ratio	Lower 95% CI	Upper 95% CI
Bobolink	Age	−0.182	0.372	0.83	0.40	1.73
	Age^2	0.021	0.026	1.02	0.97	1.07
	Age^3	−0.001	0.001	1.00	1.00	1.00
	Date	0.024	0.025	1.02	0.98	1.08
	Parasitized	1.847	0.448	6.34	2.63	15.26
Clay-colored sparrow	Age	0.627	0.281	1.87	1.08	3.24
	Age^2	−0.050	0.021	0.95	0.91	0.99
	Age^3	0.001	0.001	1.00	1.00	1.00
	Days grazed	0.009	0.008	1.01	0.99	1.03
	Interval grazed	−0.114	0.093	0.89	0.74	1.07
	Initial overhead concealment	−0.048	0.029	0.95	0.90	1.01
	Date	−0.020	0.009	0.98	0.96	1.00
	Litter	−0.004	0.037	1.00	0.93	1.07
	Parasitized	0.621	0.257	1.86	1.12	3.08
	Treatment	−0.064	0.088	0.94	0.79	1.11
	Visual obstruction	0.187	0.072	1.21	1.05	1.39
Savannah sparrow	Age	0.790	0.340	2.20	1.13	4.29
	Age^2	−0.059	0.024	0.94	0.90	0.99
	Age^3	0.001	0.001	1.00	1.00	1.00
	Cover	0.303	0.324	1.35	0.72	2.55
	Days grazed	−0.015	0.020	0.99	0.95	1.03
	Edge density	0.000	0.001	1.00	1.00	1.00
	Interval grazed	−0.583	0.220	0.56	0.36	0.86
	Initial overhead concealment	0.011	0.028	1.01	0.96	1.07
	Date	−0.013	0.010	0.99	0.97	1.01
	Litter	0.005	0.054	1.00	0.90	1.12
	Parasitized	0.435	0.315	1.55	0.83	2.86
	Treatment	0.114	0.271	1.12	0.66	1.91
	Visual obstruction	0.252	0.151	1.29	0.96	1.73

predators (Grant et al. 2006). In addition, parasitism was not always lethal to host young. Clay-colored sparrows simultaneously fledged host and cowbird young as often as cowbirds caused complete loss of host young (13 instances each). We believe, however, that brown-headed cowbirds likely impact host productivity via egg and nestling removal (Granfors et al. 2001, Kerns 2004).
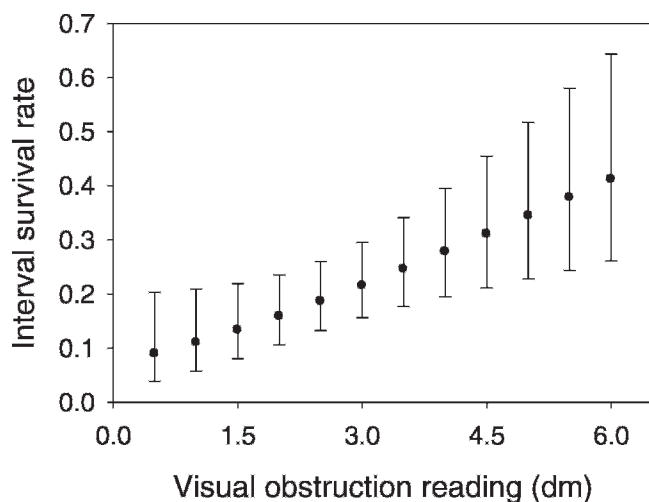
Winter et al. (2005) also found clay-colored sparrow nest success increased with increasing nest cover. Taller, denser shrubs and associated vegetation may afford clay-colored sparrow nests better concealment from predators. Tall and dense vegetation may also allow clay-colored sparrows to place their nests higher in shrubs, where nests are less likely to be encountered by small, ground-dwelling animals that depredate nests (Grant et al. 2006). Contrary to our expectation, bobolink and savannah sparrow nest survival did not exhibit a clear relationship with vegetation height
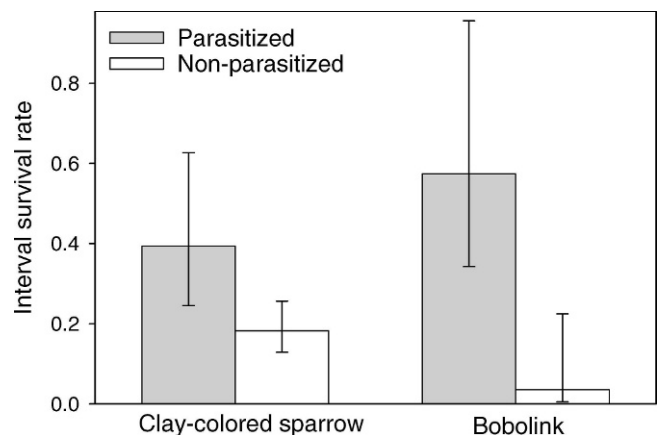

Figure 2. Effect of nest-site vegetation height and density, as measured via visual obstruction of a Robel pole (Robel et al. 1970), on nesting interval survival, with 95% confidence intervals, of clay-colored sparrow nests in northwestern North Dakota, USA, 2002–2003.

Figure 3. Effect of parasitism by brown-headed cowbirds on nesting interval survival, with 95% confidence intervals, of clay-colored sparrow and bobolink nests in northwestern North Dakota, USA, 2002–2003.
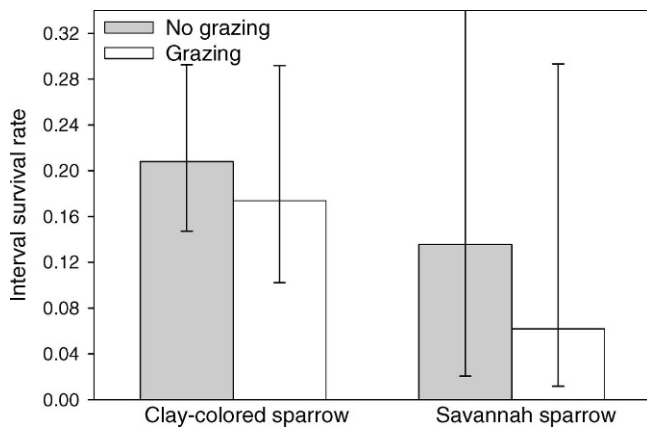
Figure 4. Effect of interval grazing (cattle present during observation) on nesting interval survival, with 95% confidence intervals, of clay-colored and savannah sparrow nests in northwestern North Dakota, USA, 2002–2003.

and density. Savannah sparrows choose nest sites with higher vegetation height and density (Dieni and Jones 2003, Davis 2005) but this characteristic has not been associated with nest survival. Both Davis (2005) and Winter et al. (2005) found significant variation in vegetation effects on nest survival among grassland passerines.

Most features composing our cover variable were woody cover. In the mixed-grass prairie, clay-colored sparrow nest survival was greater near woody edges where abundance of 13-lined ground squirrels (*Spermophilus tridecemlineatus*), an important nest predator, was lower (Grant et al. 2006). In tall-grass prairie, proximity to woody cover can negatively affect density and nest success (Johnson and Temple 1990, Temple et al. 1999, Fletcher and Koford 2003). In contrast to many prairie sites, our sites were less fragmented and had little woody encroachment. These differences may explain the lack of support for effects of edge and cover, although woody cover may affect nest survival at higher spatial scales than we measured.

We detected evidence that grazing as currently used to restore northern mixed-grass prairie at national wildlife refuges negatively impacted the nesting success of savannah sparrows, and may have impacted that of clay-colored sparrows. Bobolink nest survival apparently was not impacted, but their nest survival was so low (3.5%) that effects due to grazing may have been difficult to detect. The variability of species' responses to cattle presence during the nesting period could be the result of nonrandom distribution of cattle within grazing cells. If cattle spent disproportionately more time in some areas (our qualitative impression) and, hence, more time near certain nests, a spatially dependent effect on nest survival could result. The actual mechanism by which the presence of cattle might negatively affect nests is unclear, but could be related to disturbance and, thus, more frequent movements of small predators, or repeated flushing of adults at the nest. Trampling was not the cause, as evidenced by the small percentage of nests affected. The number of days of grazing prior to each nest observation had no relationship to nesting survival,

suggesting the cumulative effect of cattle on nest survival was negligible. Temple et al. (1999) reported savannah sparrow density and nest success were less in grazed versus ungrazed pastures in Wisconsin, USA. However, the stronger negative effect they measured was likely related to shorter grazing rotations and higher stocking rates than those in our study.

MANAGEMENT IMPLICATIONS

Land managers should consider possible short-term risks to breeding birds, especially those of high conservation concern, when designing restoration and maintenance plans for mixed-grass prairies. Grazing is a valuable tool to increase heterogeneity within grasslands, which is necessary to accommodate a wide range of grassland wildlife species (Ryan 1990, Madden et al. 2000). By limiting the area actively grazed during each breeding season, managers may reduce nest mortality of passerines, but important caveats are 1) the rotational grazing we studied was implemented on public conservation lands in accordance with established guidelines, 2) study sites were ungrazed for 2 years prior to this study, and 3) our study spanned only 2 years. We have no information regarding the effects of more intense or prolonged grazing.

We believe 2 important aspects of mixed-grass prairie avian ecology require additional study. The temporal patterns we observed likely reflect large-scale mechanisms, such as predator–prey dynamics, which may affect all upland-nesting passerines to some degree. These dynamics cannot be fully understood without additional knowledge of nest predators and the factors that influence predator communities at different scales. Finally, our results should not be applied to wetland-associated, mixed-grass prairie passerines, such as the Nelson's sharp-tailed sparrow (*Ammodramus nelsoni*) or LeConte's sparrow (*A. leconteii*). We observed that cattle thoroughly grazed wetland sites and nest survival of the aforementioned species could have been more substantially impacted.

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Associate Editor: Twedt.